

homozygotes, positive assortative mating is therefore unlikely to apply in this case. WAHLUND's effect and restricted neighbourhood size may play some role but an inbred maternal population is likely to be the dominant cause. Only stand 39 produced an excess of homozygotes and the reason for a more highly inbred maternal population in this stand than in the others is not apparent.

References

BOYLE, T. J. B. and E. K. MORGENSTERN: The population structure of black spruce in central New Brunswick. Proc. 29th Northeast. For. Tree Imp. Conf., Morgantown, WV: 142–156 (1985a). — BOYLE, T. J. B. and E. K. MORGENSTERN: Inheritance and linkage relationships of some isozymes of black spruce in New Brunswick. Can. J. For. Res. 15: 992–996 (1985b). — BROWN, A. H. D.: Isozymes, plant population genetic structure and genetic conservation. Theor. Appl. Genet. 52: 145–157 (1978). — BROWN, A. H. D. and R. W. ALLARD: Estimation of the mating system in open-pollinated maize populations using isozyme polymorphisms. Genetics 66: 133–145 (1970). — BROWN, A. H. D., A. C. MATHESON and K. G. ELDRIDGE: Estimation of the mating system of *Eucalyptus obliqua* L'HERIT. by using allozyme polymorphisms. Aust. J. Bot. 28: 931–949 (1975). — CHELIAK, W. M.: Temporal aspects of the mating system of *Pinus banksiana*. PhD dissertation, University of Alberta (1983). — CHELIAK, W. M., K. MORGAN, C. STROBECK, F. C. YEH and B. P. DANCIC: Estimation of mating system parameters in plant populations using the EM algorithm. Theor. Appl. Genet. 65: 157–161 (1983). — EL-KASSABY, Y. A., F. C. YEH and O. SZIKLAI: Estimation of the outcrossing rate of Douglas fir (*Pseudotsuga menziesii* [MIRB.] FRANCO) using allozyme polymorphisms. Silvae Genet. 30: 182–184 (1981). — FYFE, J. L. and N. T. BAILEY: Plant breeding studies in leguminous forage crops. I Natural cross-breeding in winter beans. J. Agric. Sci. 41: 371–378 (1951). — HEINSELMAN, M. L.: Silvical characteristics of black spruce (*Picea mariana*). USDA For. Serv., Lake States For. Exp. Sta. Paper 45: 1–30 (1957). — JAIN, S. K.: Population structure and the effects of breeding system. In: O. H. FRANKEL and J. G. HAWKES (eds.). Crop Genetic

Resources for Today and Tomorrow. Camb. Univ. Press, Cambridge: 15–36 (1975). — JAIN, S. K.: Estimation of outcrossing rates: some alternative procedures. Crop Sci. 19: 23–26 (1979). — MITTON, J. B., Y. B. LINHART, J. L. HAMRICK and J. S. BECKMAN: Observations on the genetic structure and mating system of ponderosa pine in the Colorado Front Range. Theor. Appl. Genet. 51: 5–13 (1977). — MITTON, J. B., Y. B. LINHART, M. L. DAVIS and K. B. STURGEON: Estimation of outcrossing in ponderosa pine, *Pinus ponderosa* LAWS., from patterns of segregation of protein polymorphisms and from frequencies of albino seedlings. Silvae Genet. 30: 117–121 (1981). — MORGENSTERN, E. K.: Preliminary estimates of inbreeding in natural populations of black spruce, *Picea mariana*. Can. J. Genet. Cytol. 14: 443–446 (1972). — PARK, Y. S. and D. P. FOWLER: Inbreeding in black spruce (*Picea mariana* [MILL.] B. S. P.): self-fertility, genetic load and performance. Can. J. For. Res. 14: 17–21 (1984). — RITLAND, K. and S. K. JAIN: A model for the estimation of outcrossing rate and gene frequencies using n independent loci. Heredity 47: 35–52 (1981). — SARVAS, R.: Investigations on the flowering and seed crop of *Pinus silvestris*. Comm. Inst. For. Fenn. 53: 1–198 (1962). — SHAW, D. V. and R. W. ALLARD: Analysis of mating system parameters and population structure in Douglas-fir using single-locus and multi-locus methods. In: M. T. CONKLE (ed.). Proc. Symp. on Isozymes of N. American Forest Trees and Forest Insects. USDA For. Serv. Gen. Tech. Rep. PSW-48: 18–22 (1981). — SHAW, D. V. and R. W. ALLARD: Estimation of outcrossing rates in Douglas fir using isozyme markers. Theor. Appl. Genet. 62: 113–120 (1982). — SHAW, D. V. and A. H. D. BROWN: Optimum number of marker loci for estimating outcrossing in plant populations. Theor. Appl. Genet. 61: 321–325 (1982). — SHAW, D. V., A. L. KAHLER and R. W. ALLARD: A multi-locus estimator of mating system parameters in plant populations. Proc. Nat. Acad. Sci., Washington, USA 78: 1298–1302 (1981). — SOKAL, R. R. and F. J. ROHLF: Biometry. Freeman, San Francisco (1969). — SQUILLACE, A. E.: Average genetic correlations among offspring from open-pollinated forest trees. Silvae Genet. 23: 149–156 (1974). — STERN, K. and L. ROCHE: Genetics of forest ecosystems. Springer-Verlag, New York (1974). — STROBECK, C.: Partial selfing and linkage: The effect of a heterotic locus on a neutral locus. Genetics 92: 305–315 (1979). — WRIGHT, S.: The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 19: 395–420 (1965).

Genetic Parameters of Blue Spruce (*Picea pungens*) at Two Locations in Michigan¹⁾

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Abstract

One hundred sixty three open-pollinated families from 42 stands from throughout the natural range of blue spruce were grown at two test sites in Michigan. Within and between stand variance components, family heritabilities, and genetic correlations were calculated for height, foliage color and time of bud-burst. Results at both sites were, for the most part, similar. Except that no geographic variation was detected for height in the northern test (probably because cold damage reduced the growth of trees from southern origins there), family variation for height and foliage color was approximately equally divided among geographic regions, stands within regions and families within stands. For bud burst, measured only in the southern Michigan test, family within stand variation was twice as great as the regional or stand within region components. Estimates of genetic components of variation derived from these results indicate that within stand genetic variation is

approximately twice as great as between stand genetic variation for height and foliage color, while within stand genetic variation is eight times greater than between stand genetic variation for bud-burst. Family heritabilities for height and foliage color were about 0.5, and for bud-burst about 0.8. Genetic correlations were small, but significant for foliage color with height and bud-burst.

These results were used to develop a possible first generation selection strategy for blue spruce which utilizes within and between stand genetic variation.

Key words: selection, tree breeding, genetic correlations, heritability.

Zusammenfassung

Auf zwei Teststandorten in Michigan wurden 163 Familien aus freier Abblüte von 42 *Picea pungens* Beständen aus dem gesamten natürlichen Verbreitungsgebiet angebaut. Nach Messung der Höhe und Feststellung der Nadelfarbe und des Knospenaustriebes nach 4 Jahren wurden die Variationskomponenten zwischen und innerhalb der Bestände, die Familien-Heritabilitäten und die genetische Korrelation berechnet. Für beide Anbaustandorte waren die Ergebnisse größtenteils ähnlich. Außer daß im nörd-

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lichen Versuch für die Höhe keine geographische Variation zu finden war, (wahrscheinlich weil dort Frostschaden das Wachstum der südlichen Herkünfte reduzierte), war die Familienvariation für Höhe und Nadelfarbe annähernd gleichmäßig zwischen den geographischen Regionen, den Beständen, innerhalb der Regionen und den Familien innerhalb der Bestände verteilt. Für den Austrieb, der nur im Versuch in Südmichigan bonitiert wurde, war die Variation der Familien innerhalb der Bestände zweimal so groß wie die regionale Variation oder diejenige innerhalb der Regionalkomponenten. Schätzungen für die genetischen Variationskomponenten, die von diesen Ergebnissen abgeleitet wurden, zeigen an, daß die genetische Variation innerhalb der Bestände annähernd zweimal so groß ist wie die genetische Variation zwischen den Beständen für die Höhe und die Nadelfarbe, während die genetische Variation für den Austrieb innerhalb der Bestände achtmal größer ist als zwischen den Beständen. Die Familienheritabilitäten für Höhe und Nadelfarbe waren etwa 0,5 und für den Austrieb 0,8. Die genetischen Korrelationen waren klein, aber für die Nadelfarbe mit Höhe und Austrieb signifikant. Die Ergebnisse wurden benutzt, um für die erste Generation eine Selektionstrategie für *Picea pungens* zu entwickeln, welche innerhalb und zwischen der genetischen Bestandesvariation von Nutzen ist.

Introduction

When a species is to be domesticated, knowledge of its genetic architecture--the degree and patterns of variation, inheritance and genetic correlations among traits--is essential to planning an effective breeding strategy (LIBBY,

1973). Accumulating this information requires much research and consumes considerable time. Breeders are, therefore, forced to begin selection efforts with incomplete genetic knowledge.

A common solution, particularly with exotics, has been to describe the geographic variation patterns, select at this level first, and select within the best geographic zones subsequently.

Another solution is to initiate tree breeding efforts with a range-wide provenance-progeny test. Such tests provide information on the distribution of variances within and between stands, heritabilities, and genetic correlations in addition to geographic variation patterns. This is not complete knowledge of the species genetic architecture, but it does allow the design of first generation selection strategies that utilize both within and between stand sources of variation, and it also indicates promising directions for future selection efforts.

In this paper range-wide provenance-progeny test results were used to devise first generation selection strategies for blue spruce. Blue spruce is a native of the central and southern Rocky Mountains (*Figure 1*), where it is usually confined to riparian zones and is rarely cut for timber. However, large quantities are grown for ornamental purposes and Christmas trees. For these purposes, improvement in growth rate, increased percentage of trees with blue (waxy) foliage, and late bud-burst to reduce damage from spring frosts are highly desirable. In some areas winter cold tolerance may be an important selection criterion (BONGARTEN and HANOVER, 1986).

The geographic patterns of variation in blue spruce, based on provenance tests at eight locations, have been reported in a previous paper (BONGARTEN and HANOVER, 1986). Patterns were different for each of the traits examined. Growth rate generally increased with declining latitude of origin, while bud-burst was latest in trees from the western portions of the range (Utah and northern Arizona). Foliage blueness was maximized in northern Arizona and New Mexico and southern Colorado, declining northward or southward. Winter needle injury was observed only on trees from the southernmost origins. These patterns were similar at each test site except that trees of southern origin were comparatively smaller at the coldest site than at the other test sites.

The provenance tests have identified no region or specific set of stands which have the desired combination of traits. Furthermore, as will be shown in this paper, within stand variation accounts for a large proportion of the genetic variation. Under these circumstances, the advantage of provenance-progeny tests for first generation selection is particularly apparent. The present work is a specific example of the development of a first generation breeding strategy which utilizes information and materials generated from provenance-progeny tests established at the outset of an improvement program.

Materials and Methods

Blue spruce seeds were collected in the fall of 1969 from wind pollinated cones on individual trees in 42 stands throughout the natural range (*Figure 1*). From two to ten trees were sampled in each stand, the average being 3.9. The seeds from each tree were kept separate and are considered to constitute half-sib families, randomly mated within stands.

The seeds were sown in an East Lansing, Michigan nursery in the spring of 1970. A randomized complete block

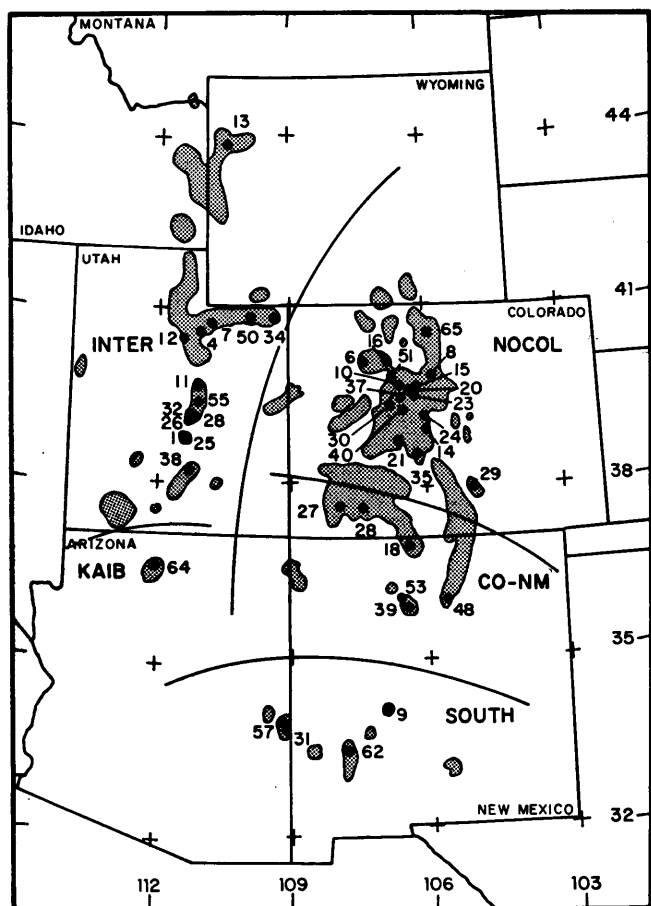


Figure 1. — Distribution of stands used in the provenance-progeny test with the regional designations developed by BONGARTEN and HANOVER (1985). Shaded area represents the natural range of blue spruce

Table 1. — Regional and plantation means for height and foliage color.

Region	Height: % of test mean and (cm)		Foliage Color (Scale: 0=green to 12=blue)		Bud burst Kalamazoo
	Kalamazoo	Chippewa	Kalamazoo	Chippewa	
Intermountain	94 (69)	91 (32)	4.5	3.6	18.4
Northern Colorado	94 (70)	102 (36)	5.1	4.4	21.6
So. Colorado - No. New Mexico	111 (82)	106 (37)	6.8	6.1	24.1
So. Arizona - New Mexico	121 (90)	101 (35)	4.7	3.9	25.3
Kaibab	101 (75)	100 (35)	7.9	7.3	16.8
ALL	100 (74)	100 (34.5)	5.2	4.5	21.7

design of four replicates was used. In each replicate half-sib family row plots 117 cm long containing 20 seeds were established. The rows were 10 cm apart.

The seedlings were grown in the nursery for three years. In the spring of 1973, they were lifted and half-sib progeny tests were established at two locations: one in Kalamazoo County, Michigan and one in Chippewa County, Michigan. At both sites the planting design was three randomized complete blocks with four tree row plots. Tree spacing was 1.8 m × 2.4 m.

The two test locations differ substantially in their climatic and edaphic conditions. The Kalamazoo site in southern Michigan (latitude: 42°20', longitude 85°20') is warmer than the Chippewa site in northern Michigan (latitude: 46°10', longitude: 84°21'). The average January temperature at the Kalamazoo site is -4° C; for the Chippewa site it is -10° C. July averages are 23° C and 18° C respectively. The Kalamazoo site also has a longer frost-free period: 153 days versus 143 (USDA, 1941). The Kalamazoo site is more fertile and received greater care. The soil is an agricultural quality sandy loam. Strip weed control was used to reduce competition around the trees, and mowing was practiced several times each year between rows. The Chippewa test is on a deep sandy soil of low fertility. The only weed competition is bracken fern and no weed control was necessary. The differences in conditions resulted in the Kalamazoo County trees being more than twice as tall as the Chippewa County trees (Table 1). Nevertheless, survival was somewhat greater in the Chippewa County test, 90% to 85%.

Bud-burst and foliage color were measured in the Kalamazoo plantation in the spring of 1977. Heights in both plantations and foliage color in the Chippewa plantation were measured in the autumn of 1977. Heights in each

plantation were analyzed on plot means. Color was scored on a scale of 0 = green to 3 = blue for each tree. Plot sums (adjusted for mortality by extrapolation) were calculated and these data were used for analyses at each site individually. For the analysis of the two tests together, heights and foliage color scores were converted to standard normal deviates in each plantation to homogenize error variances. Bud-burst was measured on a scale from 0 = no activity to 10 = fully flushed for each tree on April 29, 1977. Plot means × 10 were the units of analysis.

Family variation was divided into three components: regions, stands within regions and families within stands. Regions were those defined in BONGARTEN and HANOVER (1986) based on variation patterns in height, foliage color, time of spring bud-burst, and winter damage in eight provenances tests (Figure 1).

The full model for the analysis was:

$$Y = \bar{\mu} + S_i + B(S)_{j(i)} + R_k + p(R)_{l(k)} + f(p)_{m(l)} + SR_{ik} + Sp(R)_{il(k)} + Sf(p)_{im(l)} + *jklm(i)$$

where:

- $\bar{\mu}$ = experiment mean
- S_i = test site effects
- $B(S)_{j(i)}$ = block within site effects
- R_k = region effects
- $p(R)_{l(k)}$ = stand within region effects
- $f(p)_{m(l)}$ = family within stand effects
- SR_{ik} = region × test site effects
- $Sp(R)_{il(k)}$ = stand within region × test site effects
- $Sf(p)_{im(l)}$ = family within stand × test site effects
- $*jklm(i)$ = residual (family by block within test site effects)

Table 2. — Variance components (± standard errors) for eight year height, foliage color and spring bud-burst at the Kalamazoo County test site. All components are significant at the $\alpha = 0.0001$ level.

Source of Variation	d.f.	Height		Foliage Color		Bud-burst	
		cm ²	% of Fam. Var.	Units ² ^{1/}	% of Fam. Var.	Units ² ^{2/}	% of Fam. Var.
Blocks	2	-	-	-	-	-	-
Families	162	88.93 ± 12.00	100	2.74 ± 0.32	100	20.02 ± 2.33	100
Stands	41	61.94 ± 16.48	70	1.90 ± 0.50	69	9.55 ± 2.82	48
Regions	4	33.24 ± 16.89	37	0.61 ± 0.52	22	4.24 ± 3.18	21
Stands (Regions)	37	28.70 ± 8.93	32	1.29 ± 0.29	47	5.30 ± 1.92	27
Families (Stands)	121	26.99 ± 7.18	30	0.84 ± 0.20	31	10.47 ± 1.66	52
Error	312	79.13 ± 6.34		2.01 ± 0.16		7.12 ± 0.57	

^{1/} Units are from 0=green to 12=blue.

^{2/} Units are from 0=no buds flushed to 10=all buds flushed.

Table 3. — Variance components (\pm standard errors) for eight year height and foliage color at the Chippewa County test site. All components are significant at the $\alpha = 0.0001$ level except for the regional component of height.

Source of Variation	d. f.	Height		Foliage Color	
		cm ²	% of Fam. Var.	Units ^{1/2}	% of Fam. Var.
Block	2	-	-	-	-
Families	162	26.16 \pm 4.38	100	2.26 \pm 0.29	100
Stands	41	15.90 \pm 4.96	60	1.66 \pm 0.43	74
Regions	4	1.32 \pm 6.60	5	0.66 \pm 0.47	29
Stands (Regions)	37	14.48 \pm 4.23	55	1.01 \pm 0.26	45
Families (Stands)	121	10.36 \pm 3.59	40	0.60 \pm 0.16	26
Error	316	47.05 \pm 3.74		1.70 \pm 0.14	

^{1/2} Units are from 0=green to 12=blue.

For the analysis of variance at each test site individually, the terms with site were dropped. Approximate standard errors of the variance components were calculated according to the methods in NAMKOONG (1979, pp. 229—230).

Family heritabilities and genetic correlations were determined using the family within stand terms to estimate family variances and covariances. Within plot variances were not included in the heritability calculations. Therefore, the heritability estimates are inflated, but not substantially so (WRIGHT, 1976). Heritability estimates are also somewhat overestimated because the open pollinated families are likely to contain some products of inbreeding (SORENSEN, 1973, NAMKOONG, 1966). Approximate standard errors of the heritabilities were calculated from methods described by NAMKOONG (1979, pp. 232—233). Standard errors of the genetic correlations were calculated according to the formulae in BECKER (1984, pp. 114—115).

Results

Variance Components

Height. Family variation at both test sites was highly significant. The standard deviation of family means was 15% of the plantation mean in the Kalamazoo County test and 13% of the plantation mean in the Chippewa County test.

In the Kalamazoo County plantation, family variation was nearly equally divided among regions, stands within regions and families within stands (Table 2). Over the entire geographic range, stands accounted for 70% of the family variation and families within stands for the remaining 30%.

In the Chippewa County test, stands within regions and families within stands had nearly equal variances, but no variation was detected among regions. The absence of regional variation resulted in less overall family variation (as a percent of the error variation) in the Chippewa test compared to the Kalamazoo test. However, the stands within regions and families within stands components were quite comparable at the two test sites when expressed as percent of error variation.

The absence of regional variation at the Chippewa site is thought to result from winter cold injury. Southern trees were the tallest in the milder Kalamazoo test, but they were only average at the colder Chippewa site (Table 1). The diminished growth of trees from southern provenances in northern Michigan (as compared to southern Michigan) has been observed in numerous other species as well (WRIGHT, 1973).

When both test plantations were considered together, the region \times test site interaction was, of course, highly significant. The stands within regions component was also significant, but small, and no family within stands \times test site interaction was detected. Nevertheless, over both sites, the total between stand variation was about 3.5 times greater than the family within stands component.

The within and between stand variances can be used to obtain rough comparisons of the within and between stand additive genetic variances, if a few assumptions are accepted. The between stand variance is a genetic variance comprised of additive and non-additive components which can not be separated. The family within stand variance represents one fourth of the additive-genetic variance within stands, assuming random mating. Therefore, an estimate of the within stand additive genetic component can be found by multiplying the family within stand variance by four. This estimate is somewhat inflated, particularly if there are strong dominance effects, and mating is not perfectly random (NAMKOONG, 1966). However, if we assume that dominance and interaction effects are negligible, then the between stand variance is an unbiased estimate of the additive genetic variance between stands and four times the family within stand variance is a nearly unbiased estimate of the within stand additive genetic variance (if inbreeding is not excessive). Under these assumptions, additive genetic variation within stands appears to be somewhat larger than variation among stands over the entire species range. In the Kalamazoo County test, the within stand genetic variance was almost twice as great as the total between stand genetic variance (stand within region plus region), and it was four times greater in the Chippewa County test. Over both test sites it was only 2.3 times greater. If dominance effects are important, both the within and between stand additive genetic variances will be overestimated when calculated in the above-mentioned manner; therefore, the relative proportions of the additive genetic variances may not be grossly in error in this event. However, the effect of non-additive variances is unknown and proportions of between and within stand additive variation calculated here must be considered only as rough estimates.

Foliage Color. The amount and pattern of foliage color variation was similar in the two test plantations. Genotype \times test site interaction was negligible and non-significant for each component (Table 4).

The stand within region component had the largest variance, accounting for nearly one half of the total family

Table 4. — Analysis of Variance for height and foliage color: both plantations considered together.

Source of Variation	d.f.	Height		Foliage Color	
		MS	Variance	MS	Variance
Blocks	5	1.69	<0.00	1.873	0.01
Families					
Stands	41	6.70**	0.23	10.460**	0.40
Regions	4	21.93**	0.05	44.203**	0.14
Stands (Regions)	37	5.05**	0.17	6.811**	0.25
Families (Stands)	121	1.35**	0.13	1.340**	0.15
Families x test sites					
Region x test site	4	10.58**	0.12	0.136	<0.00
Stands (Regions) x test sites	37	1.00*	0.03	0.751	0.02
Families (Stands) x test sites	121	0.66	0.03	0.484	0.02
Error	628	0.56	0.56	0.428	0.43

variance (Table 2, 3 and 4). Family within stand and region each accounted for approximately one-quarter of the family variance (Table 2 and 3). Therefore, the total between stand variance accounted for three-fourths of the total family variance and families within stands for one-fourth. The total within stand additive variance, calculated by multiplying the family within stand variance by four, was estimated at 1.8 times the total between stand genetic variance is greater than the between stand genetic variance (region plus stand within region). Standard errors indicate that the differences in the between and within stand variance components are too small to be considered significant.

Bud-burst. Bud-burst was measured only at the Kalamazoo County site. Each component of family variance in spring bud-burst was highly significant. The family within stand variance was the largest of the components account-

ing for over half of the total family variation (Table 2). The remaining variance was split almost equally among regions and stands within regions. The within stand additive variance, calculated by multiplying the family within stand variance by four, was four times greater than the between stand variance over entire species range (region plus stand within region). It is clear that the within stand genetic variance is greater than the between stand genetic variance for this trait.

Family Heritabilities and Correlations

Half-sib family heritabilities (Table 5) and genetic correlations (Table 6) were estimated based on deviations from stand means and thus represent the pooled parameters over all the random-mating populations. Family heritability for height was somewhat greater at the Kalamazoo site than the Chippewa site because the error variation was proportionally smaller. However, the estimate over both sites was greater than at either plantation individually because the genotype within stand \times environment was negligible. For foliage color, the heritability was only slightly greater than for height; the estimates were just above 0.5 at both test sites. When both tests were considered together, the estimate increased to nearly 0.7, again because genotype \times test site interaction was absent. Date of bud-burst had the highest heritability and was estimated with the greatest precision. Error variation was quite low for this trait.

Table 5. — Family heritabilities and their standard errors.

Date Base	Height	Foliage Color	Bud-burst
Kalamazoo Co.	0.50 \pm 0.08	0.55 \pm 0.07	0.81 \pm 0.03
Chippewa Co.	0.39 \pm 0.09	0.51 \pm 0.07	-
Both Plantations	0.56 \pm 0.06	0.67 \pm 0.05	-

Table 6. — Within stand genetic correlations (\pm standard errors) and between stand phenotypic correlations.

	Height	Foliage Color
Genetic Correlations with:		
Foliage Color		
at Kalamazoo Co.	0.39 (\pm 0.10)	-
at Chippewa Co.	0.11 (\pm 0.03)	-
Both sites	0.21 (\pm 0.04)	-
Bud-burst		
at Kalamazoo Co.	0.12 (\pm 0.52)	-0.19 (\pm 0.09)

Stand Correlations with:		
Foliage Color		
at Kalamazoo Co.	0.03	-
at Chippewa Co.	0.01	-
Both sites	0.02	-
Bud-burst		
at Kalamazoo Co.	0.02	0.05

All estimates of genetic correlations were low. However, foliage blueness was significantly correlated with greater height and later spring bud-burst. No genetic correlation could be shown between height and bud-burst. Correlations based on stand means as deviations from the regional means (Table 6) were quite low and non-significant. The regional patterns of variation in the three traits are also independent (Table 1).

Discussion

Generality of the Results

These results indicate that significant genetic variation occurs between regions, between stands within regions and within stands for eighth year height, foliage color and spring bud-burst. From the estimates obtained here, the within stand genetic variation for height and foliage color appears to be slightly greater than variation between

stands from the entire species range, but for bud-burst, within stand variation is much greater than between stand variation. These conclusions apply strictly only to the sites and ages of measurement. However, evidence from other experiments indicates that they may be valid regardless of site or age for foliage color and bud-burst, but not for height.

For foliage color, variation at the region, stand within region and family within stand levels does not seem dependent on site or age. No genotype \times test site interaction was detected in this study; furthermore, no interaction of consequence was detected when stand values were compared at eight locations from Nebraska to Quebec (BONGARTEN and HANOVER, 1986). Unpublished data (BONGARTEN and HANOVER) also shows foliage color to be consistent with respect to age after the first two or three years.

The relative amounts of variation for spring bud-burst are probably not dependent on site or year either. In Douglas-fir, which has been most extensively studied in this regard, the absolute amount of variance may change from year-to-year (WHITE *et al.*, 1979), from site-to-site (MORRIS *et al.*, 1957) and in different controlled environments (CAMPBELL and SORENSEN, 1978), but the genotype rankings appear to be consistent. The relative magnitudes of the within and between stand variances have also been shown to be consistent regardless of age or sites in France (CHRISTOPHE and BIROT, 1979).

On the other hand, variance components for height may change with age and site. NAMKOONG *et al.* (1972) have shown in Douglas-fir (*Pseudotsuga menziesii*) and NAMKOONG and CONKLE (1976) in ponderosa pine (*Pinus ponderosa*) that the within and between stand additive variances are altered by age or more specifically by crown development (see also FRANKLIN, 1978). A site-to-site difference in regional variation was evident in the present case. The stand within region and family within stand variances may also be subject to site variation. Genotype \times environment interaction on these levels is well established (WRIGHT, 1973; SHELBORNE, 1972), and although genotype \times environment interaction does not necessarily result in different variances at different sites, it often will. Further investigation into the time trends in height variance components is required.

Implications for Breeding

For height, foliage color and bud-burst, variation at the region, stand within region, and within stand levels is large enough to warrant selection at each level. Within stand selection appears to ultimately provide the greatest opportunity for genetic gain because of greater variability and the greater selection differentials that are possible (although several generations of selective breeding are required to capture the gain from within stand variability because only a portion of the genetic variability is present in each generation and because selection efficiency is not perfect). However, stand variation accounts for a substantial portion of the total genetic variation and first generation selection efforts should take maximum advantage of this.

The method of selection depends to a large degree on the magnitude of the heritability (FALCONER, 1980). The heritabilities calculated here are family heritabilities and indicate only the effectiveness of family selection within the progeny tests measured. However, judging from other evidence, they may be indicative of individual tree heritabilities as well. Individual tree heritability for height is well known to be low (ZOBEL and TALBERT, 1984; WRIGHT, 1976), while heritability for bud-burst appears to be high (e.g.

Picea glauca (NIENSTAEDT and TEICH, 1972) and *Pseudotsuga menziesii* (CHRISTOPHE and BIROT, 1979; REHFELDT, 1983)). Therefore, mass selection is likely to be highly effective for bud-burst and less so for height. Estimates of individual tree heritability for foliage color are not available from other species, but horticultural work suggests that foliage color is little affected by environment. Grafted scions of blue trees produce blue trees whatever the environment; trees transplanted from one location to another do not change color either. As mentioned previously, genotype \times environment interaction was negligible in a provenance test of blue spruce planted at eight sites (BONGARTEN and HANOVER, 1986). Low environmental variance indicates that broad-sense heritability, if not narrow-sense heritability, is high. Considering that foliage color is little influenced by environment, the calculated family heritabilities are actually quite modest; dominance and interaction effects appear to be important. If this is the case, phenotypic selection should be highly effective, but selection of blue trees from stands with predominantly blue trees should be more profitable than selecting equally blue trees from stands with blue and green trees because the former have a greater probability of being homozygous for genes conferring blueness.

Genetic correlations between the traits are small, but favorable for the simultaneous selection of rapid growth, blue foliage color and late spring bud-burst.

For a selective breeding program, the results from this test may be used in two ways. First, the test may be used to provide information for developing a strategy for first generation selection in the native range. Second, selections can be made within the progeny test to establish a first generation orchard. It seems likely that both would be employed. For obtaining selections from the native range, the following strategy is suggested to obtain faster growing, bluer, and later flushing blue spruce for the milder parts of the northern United States:

- 1) Selections should be restricted to the southern portion of the natural range of blue spruce.
- 2) Within this area, stands of predominantly blue trees should be identified.
- 3) Within these stands, blue trees that are late flushing should be identified.
- 4) Scions from these selected trees should be grafted into a clonal seed orchard.
- 5) Open pollinated seed from the selected trees should be collected and grown in progeny tests to provide data, especially on growth rate, for roguing the clonal orchard.
- 6) Southern stands tested in the current provenance progeny test that show below average growth rate should be avoided; northern stands which have above average growth rate in the current test could be considered.

In this scheme, selection for height occurs on the regional level by restricting selections to the southern portions of the range. A combination of between and within stand selection is also imposed by roguing on the basis of open-pollinated progeny test results. Phenotypic selection in natural stands is not emphasized because of low heritability and uneven-aged stand structure. Selection for blue foliage color occurs at the region, stand within region and within stand levels. Stand selection is emphasized because of the assumed large dominance variation. Selection for time of bud-burst is essentially limited to phenotypic selection within stands because of its high heritability and abundance of within stand variability. Grafted orchards with scions from mature trees are favored because of the lengthy ju-

venile phase in blue spruce (SAFFORD, 1974). In a breeding program for colder areas, stands from the southernmost portions of the range should be avoided. Otherwise, the same selection program could be used.

Selection within the existing progeny test could be accomplished by means of a selection index. This would require the calculation of individual heritabilities and the assigning of weights for each trait. It should also be pointed out that the family heritabilities presented here are based on within stand deviations and therefore underestimate the family heritability over all families. Family heritability could be calculated over all families, but this would be an overestimate because the families are not part of one random mating population. The effectiveness of selection within the progeny tests could be improved by increasing the number of members per family.

The emphasis placed on selection within the existing progeny tests and on selection of new materials from the native range depends on many factors. In any case, the initiation of a tree improvement program with provenance-progeny tests will lead to more rapid genetic progress in the early stages of the program than if provenance tests alone are used.

Literature Cited

BECKER, W. A.: Manual of Quantitative Genetics, Fourth Edition. Academic Enterprises, Pullman, WA. 190 p., (1984). — BONGARTEN, B. C. and J. W. HANOVER: Provenance variation in blue spruce (*Picea pungens*) at eight locations in the northern United States and Canada. *Silvae Genetica* 35: 2-3, 67-74 (1986). — CHAMPBELL, R. K. and F. C. SORENSEN: Effect of test environment on expression of clones and on delimitation of seed zones in Douglas-fir. *Theor. Appl. Genet.* 51: 233-246, (1978). — CHRISTOPHE, C. and Y. BIROT: Ge-

netic variation within and between populations of Douglas-fir. *Silvae Genet.* 28: 197-206, (1979). — FALCONER, D. S.: Introduction to Quantitative Genetics. Longman, London. 340 p., (1980). — FRANKLIN, E. L.: Model relating levels of genetic variance to stand development of four North American conifers. *Silvae Genet.* 28: 207-212, (1979). — LIBBY, W. J.: Domestication strategies for forest trees. *Can. J. For. Res.* 3: 265-276, (1973). — MORRIS, W. G., R. R. SILEN and H. IRGENS-MOLLER: Consistency of bud bursting in Douglas-fir. *J. For.* 55: 208-210, (1957). — NAMKOONG, G.: Introduction to Quantitative Genetics in Forestry. USDA, For. Serv. Tech. Bull. No. 1588. 342 p., (1979). — NAMKOONG, G.: Inbreeding effects on estimation of genetic additive variance. *For. Sci.* 12: 8-13, (1966). — NAMKOONG, G. and M. T. CONKLE: Time trends in genetic control of height growth in ponderosa pine. *For. Sci.* 22: 2-12, (1976). — NAMKOONG, G., R. A. USANSIS and R. R. SILEN: Age-related variation in genetic control of height growth in Douglas-fir. *Theor. Appl. Genet.* 42: 151-159, (1972). — NIENSTAEDT, H. and A. TEICH: Genetics of white spruce. USDA For. Serv. Res. Pap. WO-15. 24 p., (1972). — REHFELDT, G. E.: Genetic variability within Douglas-fir populations: implications for tree improvement. *Silvae Genet.* 32: 9-14, (1983). — REICOSKY, D. A. and J. W. HANOVER: Seasonal changes in leaf surface waxes of *Picea pungens*. *Amer. J. Bot.* 63: 449-456, (1976). — SAFFORD, L. O.: *Picea A. Dietr.* In: Seeds of Woody Plants in the United States (ed. C. S. SCHOPMEYER) USDA, For. Serv. Ag. Handbook No. 450. pp. 587-597, (1974). — SHELBOURNE, C. J. A.: Genotype × environment interaction: its study and its implications in forest tree improvement. *Proc. IUFRO-SABRAO Joint Symp. Tokyo.* pp. B-1(1), 1-27, (1972). — SORENSEN, F. C.: Frequency of seedlings from natural self fertilization in coastal Douglas-fir. *Silvae Genet.* 22: 20-24, (1973). — USDA: Climate and Man. Yearbook of Agriculture. U.S. Govt. Printing Office, Washington, D.C., (1941). — WHITE, T. L., K. K. CHING and J. WALTERS: Effects of provenance, years and planting location on bud burst of Douglas-fir. *For. Sci.* 25: 161-167, (1979). — WRIGHT, J. W.: Introduction to Forest Genetics. Academic Press, New York. 463 p., (1976). — WRIGHT, J. W.: Genotype × environment interaction in the north central United States. *For. Sci.* 19: 113-123, (1973). — ZOBEL, B. and J. TALBERT: Applied Forest Tree Improvement. John Wiley and Sons, New York. 505 p., (1984).

Inherent Differences in Family Response to Inter-Family Competition in Loblolly Pine

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Summary

The effects of inter-family competition on genetic parameter development and individual phenotypic response were examined. Two 20-year-old open-pollinated progeny tests of loblolly pine (*Pinus taeda* L.), and seedlings from five mother-tree families common to both tests were used to evaluate the above competitive effects. Genetic parameters from both the mature progeny tests and the seedling study changed over time. Response to competition was significantly different among families, and two indicators of competition suggested competition was occurring in all studies. However, genetic parameter changes expressed by these families were not in direct response to the onset of competition. The competition analysis revealed significant differences in the competitive abilities and competitive influences among the seedlings of the five tested families. Family S2PT10 was involved in the majority of the significant competitive effects. Transgressive overyielding and underyielding competitive effects were displayed among

the family combinations. No one family could be identified as consistently overyielding or underyielding.

Key words: Inter-family competition, competitive ability and competitive influence, genetic parameter.

Zusammenfassung

Es werden die Wirkungen von Konkurrenz auf die Entwicklung genetischer Parameter innerhalb der Familien, sowie die individuelle phänotypische Reaktion untersucht. Die Ergebnisse aus der Prüfung von zwei zwanzigjährigen frei abgeblühten Nachkommenschaften bei *Pinus taeda* L. und aus der Prüfung von Sämlingen von fünf Mutterbäumen, die in beiden Tests enthalten waren, wurden benutzt, um die oben erwähnte Konkurrenzwirkung zu bestimmen. Die genetischen Parameter von beiden, d.h. aus der Untersuchung der älteren Nachkommenschaften und der Sämlinge, wechselten über den Zeitraum. Die Reaktion auf die Konkurrenz war innerhalb der Familien signifikant unterschiedlich und zwei Konkurrenzindikatoren haben gezeigt, daß in allen Versuchen Konkurrenzeffekte auftreten sind. Die genetischen Parameterwechsel, die bei diesen Familien zum Ausdruck kamen, waren jedoch keine direkte Reaktion auf das Auftreten von Konkurrenz. Die Konkurrenzanalyse ergab signifikante Unterschiede in den

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